Gypsy Moth: Forest Influence

United States Department of Agriculture

Forest Service

Agriculture Information Bulletin No. 423

Gypsy Moth: Forest Influence

United States Department of Agriculture

Forest Service

Agriculture Information Bulletin No. 423

by
Robert W. Campbell
Research Entomologist
Pacific Northwest Forest and Range Experiment Station

The Author

Robert W. Campbell is now at the Forestry Sciences Laboratory of the Pacific Northwest Forest and Range Experiment Station, Corvallis, Oreg. At the time the studies fundamental to this report were being completed, he was on the research staff of the Northeastern Forest Experiment Station, stationed at Syracuse, N.Y., in cooperation with the Department of Forest Entomology, State University of New York, College of Environmental Science and Forestry. He received his bachelor's degree in forestry from the State University of New York College of Forestry in 1953 and his master's and Ph.D. degrees in forestry from the University of Michigan in 1959 and 1961. He joined the Forest Service's Northeastern Forest Experiment Station in 1961.

June 1979

For sale by the Superintendent of Documents, U.S. Government Printing Office
Washington, D.C. 20402

Stock No. 001–000–03928–8

Contents

Abstract

Invasion and subsequent heavy defoliation of a composite forest in eastern New England by the gypsy moth produced visual symptoms that disappeared in a few years, but secondary consequences lasted for decades. Repeated defoliation resulted in drastic alterations in the forest. Stand density dropped dramatically, and overall species composition changed. However, these changes reduced the forest's susceptibility to further defoliation and damage. Patterns of forest succession can be altered through defoliation.

Introduction

You may not realize it, but you share the forested grounds around your home with a multitude of insect neighbors. Most of these are either so inconspicuous or so rare that unless you searched them out you might not know that they are around. Unfortunately, some forest-dwelling insects are altogether *too* noticeable from time to time; the gypsy moth is one. Hungry gypsy moth caterpillars have sometimes defoliated hundreds of thousands of acres in the hardwood forests of the northeast. The resulting landscape—a naked and apparently lifeless forest in midsummer—can move even a casual visitor to tears.

How serious is the gypsy moth problem? This simple question lies at the heart of a long and sometimes bitter controversy over the proper management of this pest. Unfortunately, the answer is necessarily both complex and—for the present at least—far from complete.

Although various strains of the gypsy moth now live on at least four continents (Europe, Asia, Africa, and North America), the strain found in North America was definitely introduced from Europe in 1868 or 1869.

Introduced pests are often most destructive for a relatively short time after they first infest a new area. In early infestations, explosive and destructive populations are common. For a variety of reasons, however, the destruction often diminishes rather rapidly. Thus far, the gypsy moth has followed this pattern. Around the turn of this century, for example, it was devastating in the vicinity of Boston, Mass., where it was introduced. Accounts of the early devastation would sound like works of fiction to current residents of the Boston area, but heavy defoliation continues to be common in recently infested areas to the south and west. For example, the insect has invaded and defoliated large areas of New Jersey and Pennsylvania in recent years.

To date, the gypsy moth has invaded only a fraction of the eastern hardwood forest. For many years it appeared to be contained in New England and eastern New York State by a combination of prevailing westerly winds at about the time of hatch and natural airborne dispersal, unfavorable climatic conditions for the insect to the north, and a heavily scouted, 40-mile wide barrier zone whose western boundary was the Hudson River. Until about 1940, aggressive control action was taken against all incipient infestations found within this zone. Except during this one interlude, however, invasion of new areas has been rather steady (fig. 1). Further spread seems inevitable.

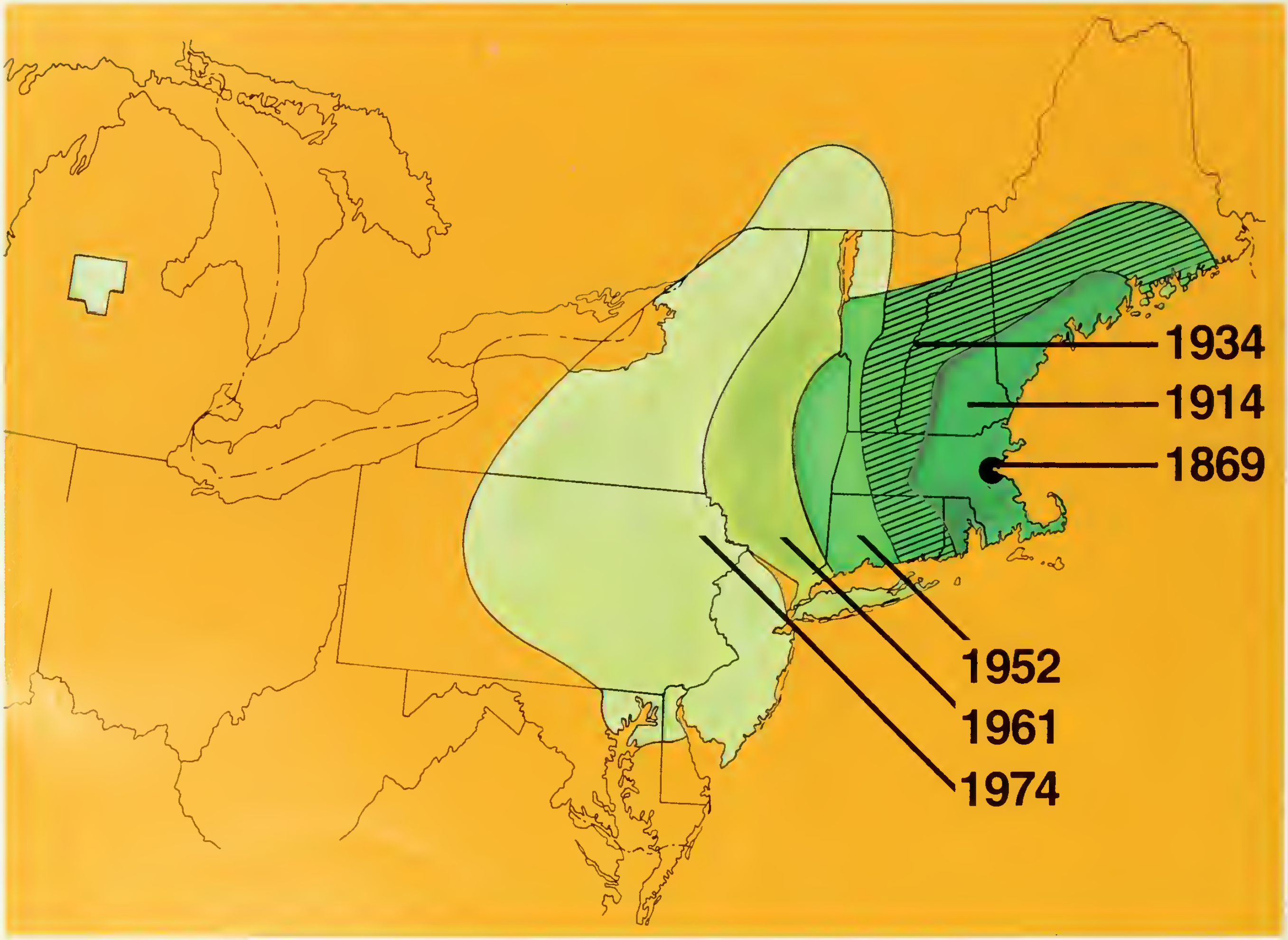


Figure 1.
Since its introduction into North America near Boston, Mass., the gypsy moth has gradually invaded more and more of the eastern hardwood forest. Early spread was more rapid toward the north and northeast. Now, however, the insect is moving rapidly into the vast hardwood forest of the Appalachian Mountains. A separate infestation is spreading in Michigan. Recently, an established infestation was found in San Jose, Calif.

Forest Invasion: A Case Study

Source data

Undoubtedly, our most complete records of relationships between defoliation by the gypsy moth and subsequent changes in the forest are those accumulated many years ago in eastern New England. The records were collected between 1911 and 1931 at the Gypsy Moth and Brown-Tail Moth Laboratory in Melrose Highlands, Mass. The laboratory was run by the former Bureau of Entomology of the U.S. Department of Agriculture.

The Melrose Highlands Laboratory is long since closed, but many of its records were never thrown away. Instead, they were moved about and stored in a variety of places between 1931 and 1970. I do not know when they were deposited in Connecticut, but they finally came to rest in a seldom-visited attic room in a beautiful old building on the campus of Yale University. Some of the records were lost in a disastrous fire that gutted the building in 1964. The records that *did* survive the fire were rediscovered in 1970, and they proved to be much more extensive than any other known sources of similar information.

These old records provided a splendid case history of how both individual trees and, ultimately, the eastern New England forest itself responded to invasion and heavy and repeated defoliation by the gypsy moth.

About 40 tree species were present in the forest plots studied by the Melrose Highlands workers, but 7 of these species were by far the most common. These seven species were white pine, red maple, gray birch, and four oaks (white, black, scarlet, and northern red oak). Foliage of all these oaks, as well as that of gray birch, is favored as food by gypsy moth caterpillars. White pine and red maple may also be defoliated on occasion.

The sequence of events described here depended on environmental conditions in the Melrose Highlands area between 1911 and 1931. Apparently, this general pattern has often been repeated as the insect has moved into new areas. Specific outcomes, however, may well prove to have been unique to that one time and place.

Defoliation

Foliage-eating insects are always present in the forest. All trees are likely to lose some of their foliage to insects every year. If gypsy moth caterpillars eat or otherwise remove less than 50 percent of the foliage from a deciduous tree, the tree will probably keep the rest of its foliage until fall. If defoliation exceeds 75 percent, though, the tree will almost certainly produce a new crop of leaves during that same growing season (fig. 2).

One defoliation and subsequent refoliation is not a particularly stressful event in the life of a healthy hardwood forest, especially if it occurs either quite early or quite late in the growing season. But the need to produce a whole new crop of leaves can put a serious drain on a tree's energy reserves if that tree is defoliated about midway through the growing season by an insect such as the gypsy moth.

Actually, while gypsy moth caterpillars have sometimes defoliated trees across hundreds of thousands of acres, we should remember that the insect is also present but *not* causing noticeable defoliation in an area many times that large. In a very general way, defoliation tends to be highest where egg mass density is high, where this density represents an increasing population, and where the tree species are preferred food for the insect. The insects also tend to cause heavier defoliation when the population has just reached outbreak levels than in subsequent years, even if equally high egg densities persist.

Realistically, forecasting defoliation by this particular insect remains more of an art than a science. Until a reliable method for forecasting defoliation is perfected, the best estimate of expected defoliation will continue to be based on experience.

Figure 2.
Within a given year, hardwood trees will seldom produce a new flush of foliage unless at least two-thirds of their original leaves have been removed. Here, the defoliated forest is shown on the left. Within a few weeks, a new crop of leaves will be produced. Unfortunately, these new leaves are an additional drain on the energy reserves of the already defoliated tree.

Tree condition: stand appearance

Since we know that defoliated trees that subsequently refoliate tend to be under greater stress than those that do not refoliate, we sorted the records for each year into two categories: light defoliation (less than 75 percent) and heavy defoliation (75 percent or greater).

Let us look first at oak trees (white, black, scarlet, and red oaks) that experienced one heavy defoliation and then remained alive for at least 10 more years (fig. 3). The percentage of the trees that were in good visual condition dropped sharply in the year following the heavy defoliation, then continued to decline slightly during the next 4 or 5 years. At the same time, the percentage of the trees that were in poor or fair condition increased.

Figure 3.
The trees in a Melrose Highland's composite oak stand, similar to this Union Co., Pa., stand, were heavily defoliated at the start of this 10-year period. Obvious visual symptoms disappeared within 1 to 2 years, but subtle reductions in tree condition were detectable for as much as a decade.

Figure 4.
Even repeated defoliations may not kill a tree, but the foliage produced by a weakened individual is likely to be small and off-color, or "chlorotic." Here, the outline of a normal-sized leaf is shown to the left around one of these small, chlorotic leaves. Also, the trees in the background exhibit a peculiar condition called "watersprouting": extensive branch dieback followed by the production of small new branches along the main bole and the larger limbs.

Although you could only detect these subtle changes statistically, the overall appearance of the stand continued to deteriorate for about 5 years. Subsequently, the trees did recover their original appearance, but not until about 10 years after the one heavy defoliation. I think this probably reflects the following sequence of events:

First, when trees have been heavily defoliated they tend to produce smaller leaves, and these leaves tend to be off color (fig. 4). Typically, small, off-color (chlorotic) leaves are produced only for a year or two after defoliation, and this alteration in the foliage may go unnoticed by most casual observers. To an experienced observer, however, off-color foliage is a clue that something unusual has happened.

Second, twigs and branches often die back after defoliation. Dieback is usually much more obvious than off-color foliage because it may cause an abrupt change in the apparent density or "thickness" of the tree crown. Subsequently, the visual appearance of the tree may deteriorate further from the actions of organisms that are apparently able to thrive only in weakened trees.

In particular, a beetle called the two-lined chestnut borer often attacks weakened branches of previously defoliated trees. While many of these beetle attacks do not kill the tree, they may continue to degrade its appearance and condition for several years. Attacks by both these beetles and pathogens such as the shoestring fungus can kill previously defoliated trees.

Tree growth and mortality: stand density

How likely is it that a heavily defoliated tree will die? Defoliation is only one of the environmental hazards to which trees are exposed, and some trees inevitably die each year, even without defoliation or any other obvious hazard. For this reason we need some sort of baseline estimate of normal tree mortality. The old Melrose Highlands records can supply this baseline (fig. 5). Figure 5 is based on the same complex of oak species that was used to develop figure 3, but none of the trees had suffered heavy defoliation for 5 years. Only about 1 percent of the trees rated in good condition at the start of the following 5-year period died, although mortality was somewhat higher among the trees rated fair or poor.

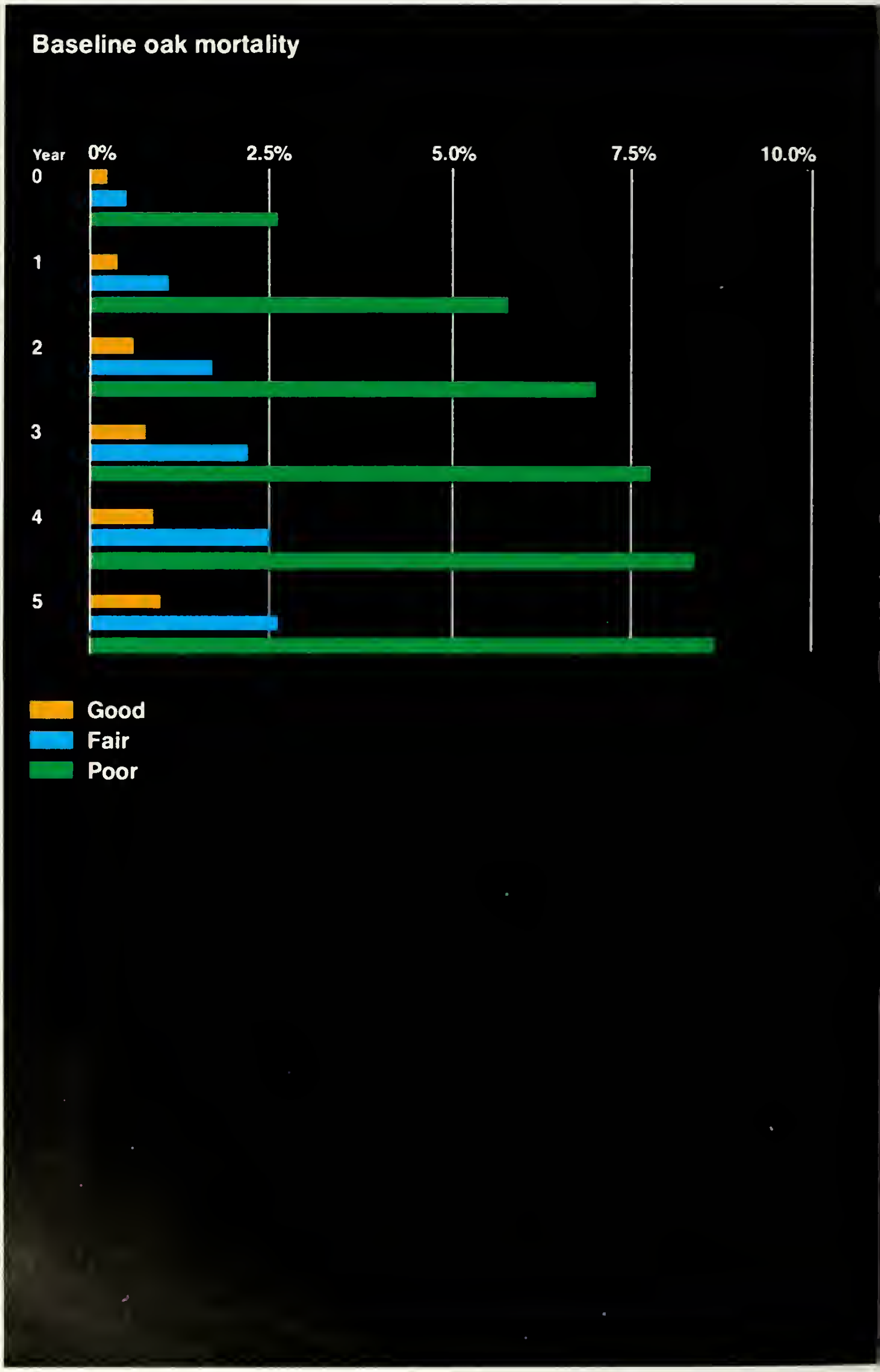


Figure 5.
Some trees die each year, even in the absence of unusual disturbance. Here, normal or "baseline" mortality is shown for a composite stand of upland oaks (white, red, black, and scarlet oak). Trees visually rated in poor condition were much more likely to die during the ensuing 5 years than those rated good. Trees whose condition was rated fair had an intermediate chance of dying.

Now let us look at 6-year mortality rates among mixed oaks that had been defoliated either once or for 2 years in succession (fig. 6). Only about 7 percent of the trees that were rated in good condition died after a single year of heavy defoliation, but about 35 percent of the trees that were rated poor died. Clearly, a tree's condition at the time of defoliation had a major bearing on the probability of its death.

Repeated heavy defoliation was followed by much higher tree mortality than a single defoliation. Not only were 55 percent of the trees that had been in poor condition dead after 5 years, but 22 percent of those rated good also died.

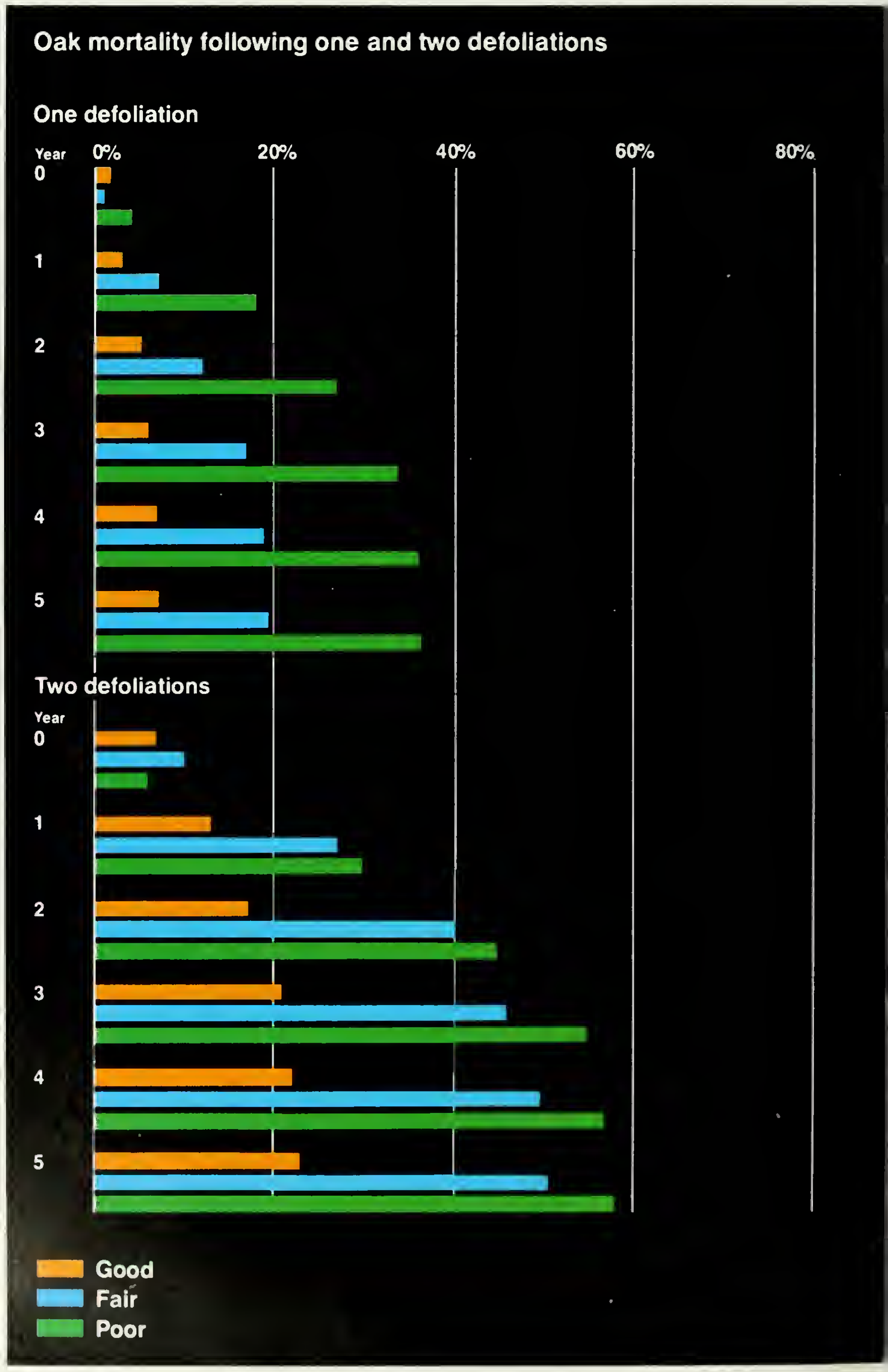


Figure 6.
Mortality among upland oaks during the 5-year period following both a single heavy defoliation and two heavy defoliations in succession. Tree condition had an important bearing on the likelihood of tree death after defoliation. Trees that were rated in poor condition were much more likely to die than those rated good. Also, two heavy defoliations in a row resulted in much higher mortality than just one.

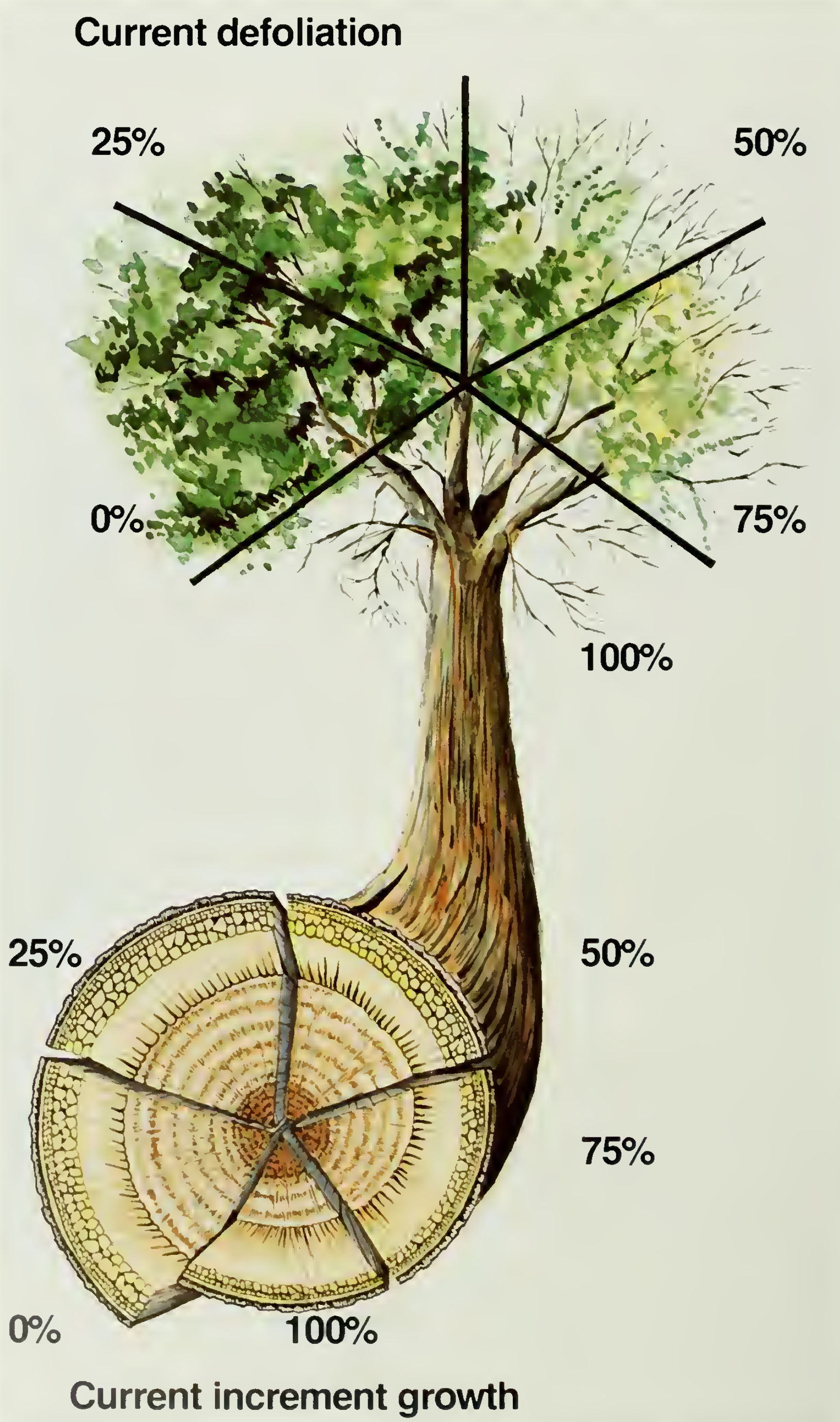


Figure 7.
Only foliage can convert energy from sunlight into a form useful to the tree. Defoliation below 50 percent has little effect on the wood produced from that energy, but woody growth along the tree bole is reduced roughly in proportion to the amount of defoliation above 50 percent. No tree is actually likely to be defoliated as shown here, but the relationship between defoliation and current woody increment would look something like this if such a defoliation pattern did occur.

Although most of the trees that were in good condition before this double attack pulled through, massive oak mortality clearly *can* follow 2 or more consecutive years of heavy defoliation. Fortunately, hardwood trees are seldom exposed to such drastic, repeated destruction of their foliage.

The relationship between a tree's foliage and the rest of the tree (twigs, branches, bole, and root system) can be likened to the relationship between capital and an investor. The foliage is like a capital investment that has been drawn from the tree's energy reserves. This investment "pays off" when energy from sunlight is converted by photosynthetic processes in the leaves and returned to the tree in a form that it can use. Defoliators like the gypsy moth represent a risk to this capital investment before the tree has acquired a fair return. Unfortunately, the ultimate bankruptcy statement is the death of the tree.

Tree mortality after defoliation is usually much more severe if it occurs just before or during an extended drought. Trees growing on drier sites, such as rocky ridges or excessively drained sands, have been subjected to much more defoliation by the gypsy moth than those growing on sites that are inherently less droughty. Interestingly, however, the trees growing on more droughty sites are *not* more likely to die following defoliation than those growing in less droughty places.

Further research will have to be done to establish many of the relations between drought, site conditions, defoliation, and tree stress physiology and mortality.

Heavy defoliation in a commercial forest can have important consequences for subsequent wood production, even when few of the trees succumb. Light defoliation has little or no effect on wood production along the tree bole, but heavy defoliation definitely reduces the production of new wood (fig. 7).

Many trees *did* succumb between 1911 and 1921 in the composite New England forest that was studied by the Melrose Highlands workers. In fact, the accelerated tree mortality and slower growth that accompanied and followed defoliation diminished the density of this composite forest by about 25 percent (fig. 8).

Changes in forest density were closely related to the percentage of oak in the stand. Only about half of the original forest density was left in 1921 in the composite stand that contained mostly oak trees. But density was only reduced by about 10 percent in stands that contained no oaks and few other favored-food species such as gray birch and quaking aspen. In the short run, this drastic decline in forest growing stock must have been catastrophic.

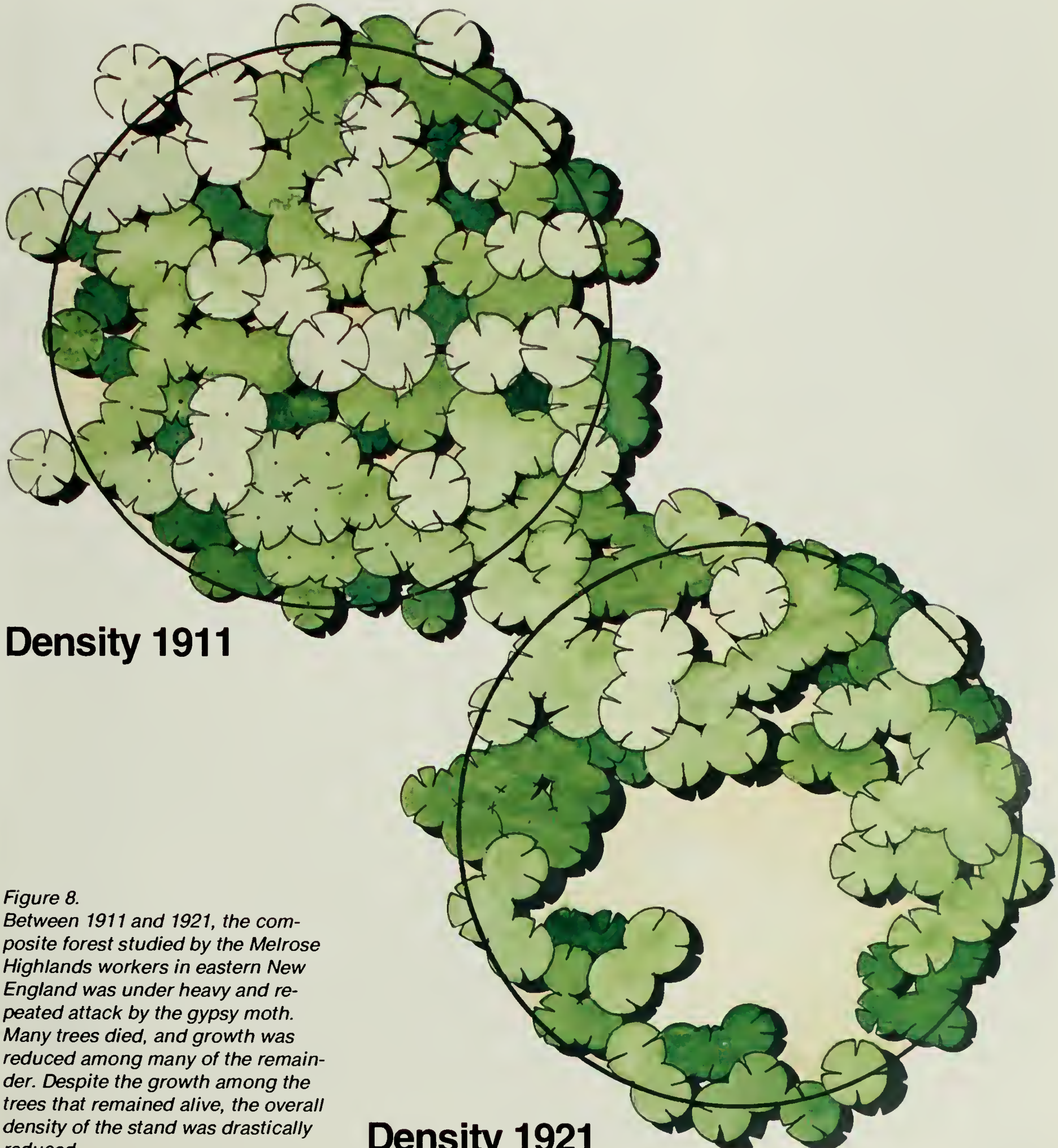


Figure 8.
Between 1911 and 1921, the composite forest studied by the Melrose Highlands workers in eastern New England was under heavy and repeated attack by the gypsy moth. Many trees died, and growth was reduced among many of the remainder. Despite the growth among the trees that remained alive, the overall density of the stand was drastically reduced.

Tree dominance: stand structure

Many of today's eastern hardwood forest stands originated as a result of a transient agriculture, heavy cutting, and wildfire. As a result, most of these stands are essentially even-aged. Nevertheless, these forests have a distinctive vertical structure (fig. 9). From a distance, the tree crowns may appear to form an even, unbroken canopy. Up close, however, one can see that some tree crowns are taller than most (or dominant), while others are shorter (suppressed). Often, one can also find a distinct shrub layer beneath the tree crowns and a more or less continuous ground cover of both woody seedlings and herbaceous plants on the forest floor itself.

Subdominant oak trees usually suffered much higher mortality than the taller dominants after a heavy defoliation (fig. 10). Only about 3 percent of the dominant trees that were rated good before one defoliation were dead 5 years later, but 12 percent of the subdominants rated good had died. Similarly, 22 percent of the dominant oak trees rated poor had died, as opposed to 41 percent of the subdominants that had been in the same condition.

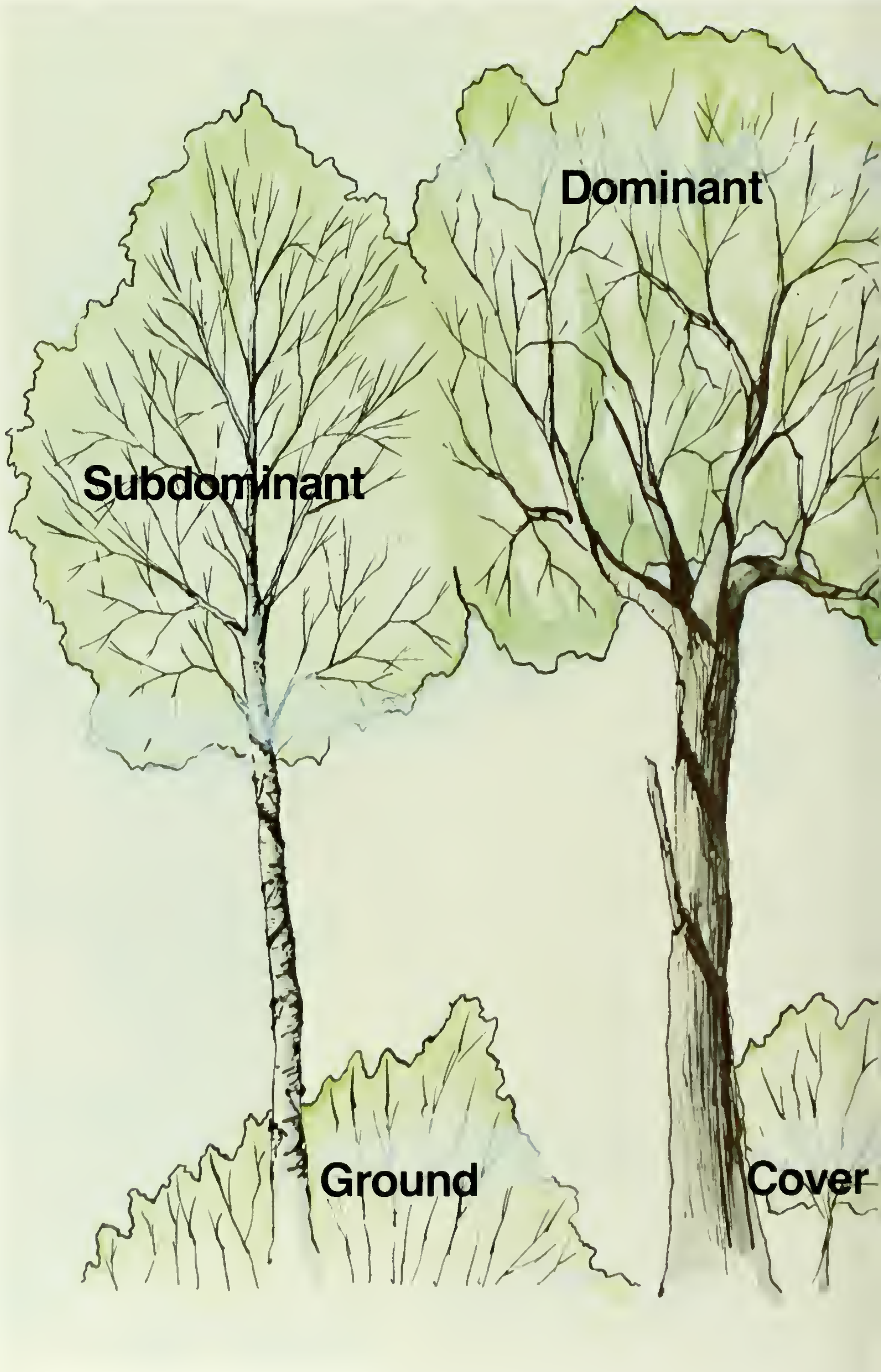
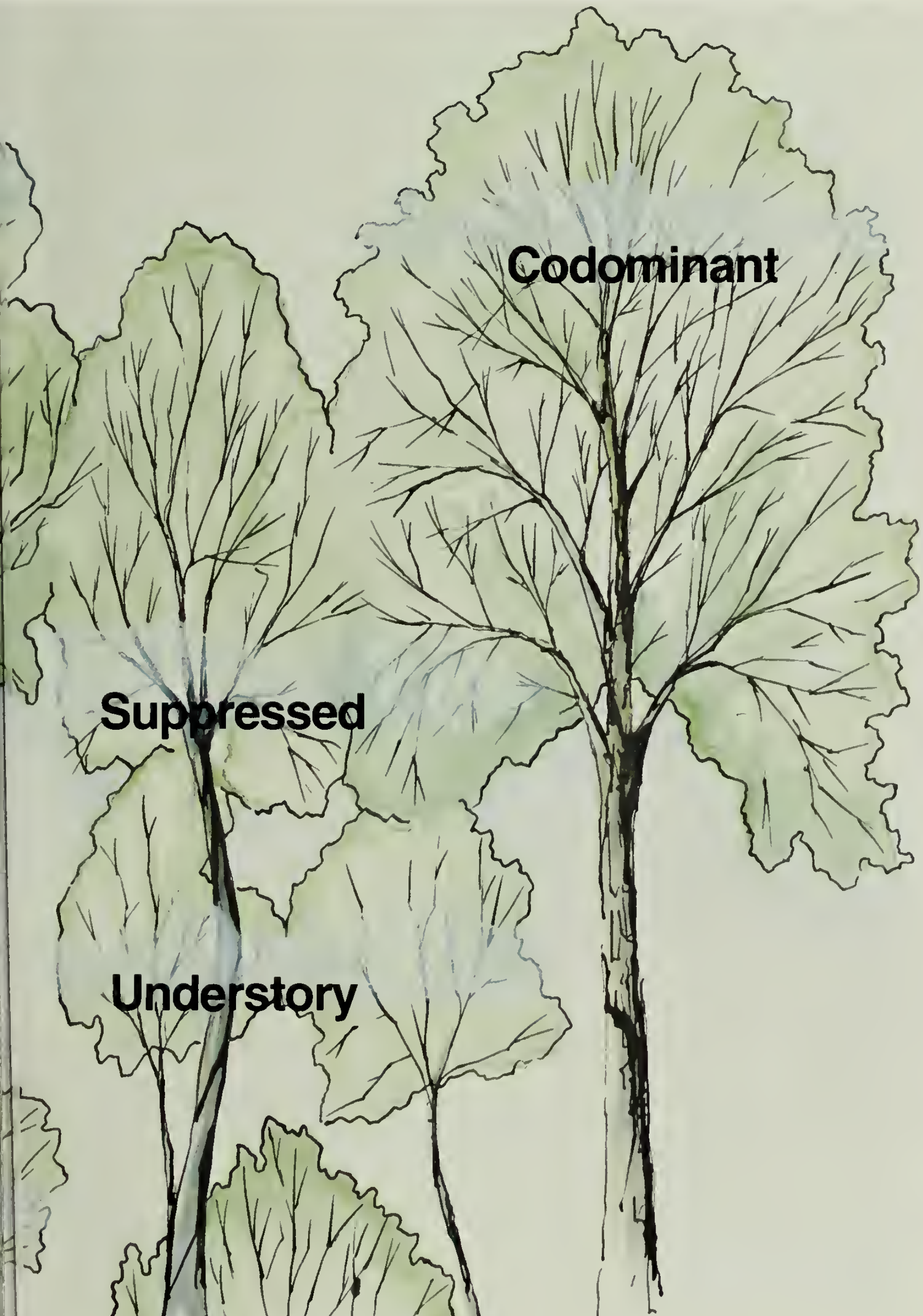


Figure 9.
The crowns of the tallest, dominant trees rise somewhat above the general level of the forest canopy. All subdominant crowns occupy somewhat subordinated positions within this canopy, and the tops of suppressed trees are below the general canopy level. Beneath this overall canopy is an understory layer of woody shrubbery, such as viburnum and mountain laurel. Typical ground cover consists of both woody seedlings and nonwoody (herbaceous) vegetation.


Codominant
Suppressed
Understory

Why should subdominant trees be more likely to die than comparable dominants, subjected to the same level of defoliation? In general, subdominant trees are more likely than dominants to be under severe stress from time to time, even without defoliation. Every green plant needs light, as well as moisture and nutrients, to maintain its life processes. The plant is said to be under stress when one or more of these basic ingredients is in short supply. Thus, the subdominant trees may already be under stress, and the added stress of defoliation tends to be more severe.

Overall, these results suggest that one heavy defoliation in an oak stand will seldom result in drastic changes. Most of the oaks that die will be sickly subdominant trees, many of which would succumb in any case. Conversely, two heavy defoliations in succession may well result in substantial tree mortality, even among healthy dominant oaks.

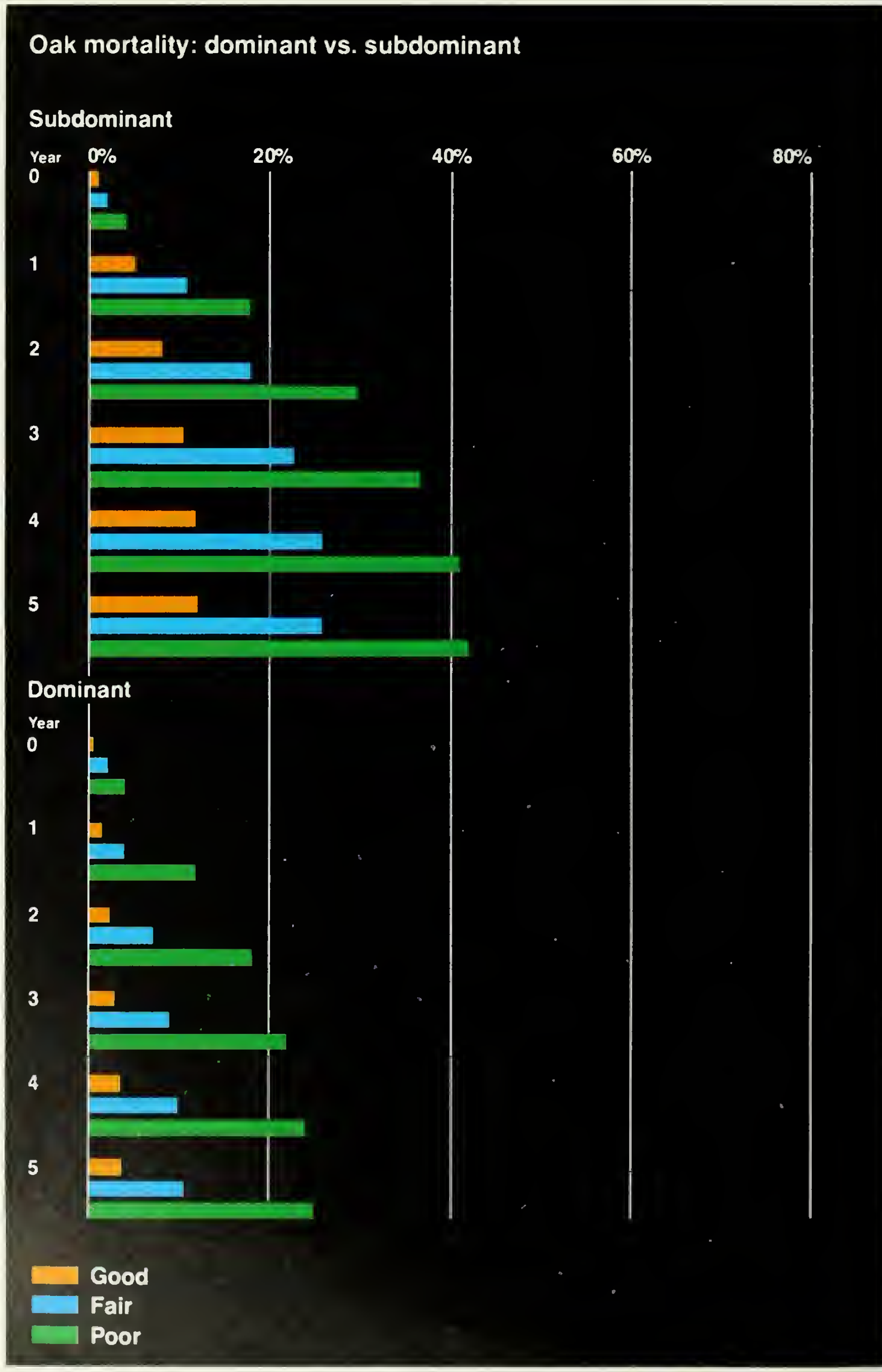


Figure 10.
On average, subdominant oak trees within the composite New England forest were more likely than dominants to die after defoliation. In this case, all of these upland oaks were subjected to one heavy defoliation. Few of the dominant trees died during the following 5 years, but mortality was heavy among the subdominants.

Trees as food: stand composition

Anyone who has watched a gypsy moth outbreak closely has probably noticed that some of the trees in a typical mixed forest are more heavily defoliated than others (fig. 11). In the forest studied by the Melrose Highlands workers, oaks (such as the white oak pictured here) and gray birch were both common and favored as food. The insects also showed a decided preference for the foliage of several less common species, such as apple. American beech, red maple, and white pine were frequently nibbled on but were rarely defoliated heavily. Eastern hemlock and pitch pine were defoliated only in the rare situations where more favored foods had been exhausted. Species such as black locust and white ash were definitely avoided.

Figure 11.
Gypsy moth caterpillars have decided food preferences. In some cases, the young insects will starve on foliage they could readily devour a few weeks later. Under outbreak conditions, the insect will nibble on the foliage of most forest tree species, but will rarely strip the foliage from the species they do not really favor unless they have already defoliated the more favored food species.

Species

Although heavy defoliation was rare among less favored tree species, when it did occur the mortality was higher among these less favored species than among the oaks (fig. 12). For example, of trees rated good before defoliation, about 7 percent of the oaks and 12 percent of the less-favored species died during the next 5 years. Mortality rates were spectacular among the less favored species that were rated poor: about 70 percent of them died after defoliation. Only about 35 percent of the comparable oak trees died during this same interval.

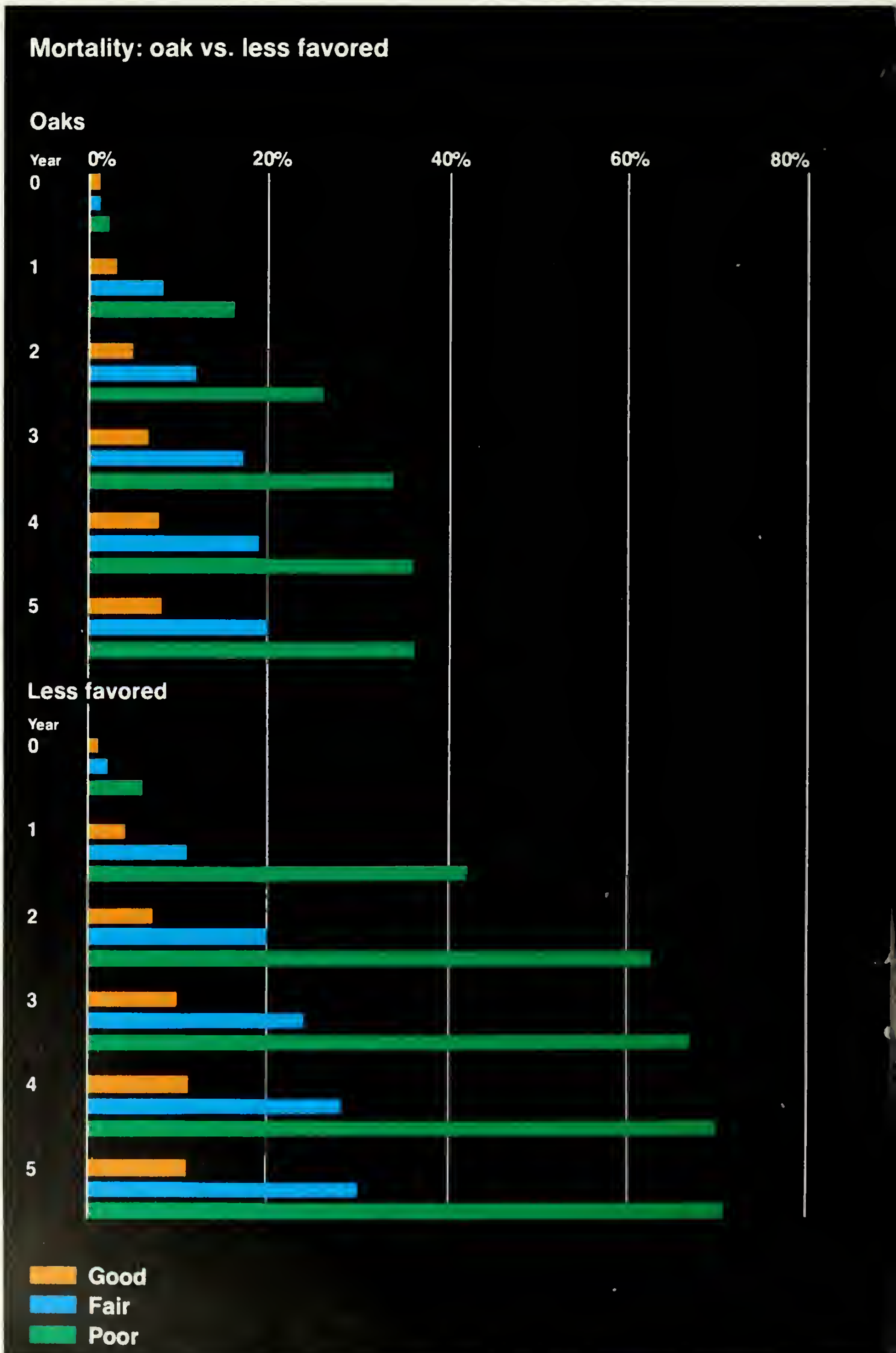


Figure 12.
Heavy defoliation of less favored trees was a relatively rare event. When it did occur, however, the consequences of the defoliation were more severe among the less favored trees than among the oaks.

In general, evergreen trees such as white pine are more readily killed by heavy defoliation than hardwood trees (fig. 13). Thus I was surprised to find that red maple trees in the Melrose Highlands forest were more likely to die after defoliation than the white pines (fig. 14). I cannot explain these substantial differences between the two species, but basic differences in either tree physiology or specific timing of events connected with defoliation could be involved. In any case, the rather low postdefoliation mortality among the white pines that were in good condition beforehand is encouraging evidence that this insect is not as serious a threat to this species as many believe.

Figure 13.
Pure pine stands are immune to defoliation by the gypsy moth. In mixture with more favored species, though, the pines may occasionally be heavily defoliated after the more favored foliage has been devoured. Here, a clump of young white pine trees has been stripped by hungry gypsy moth caterpillars. Some of these trees will probably die, but a surprisingly high percentage are likely to survive.

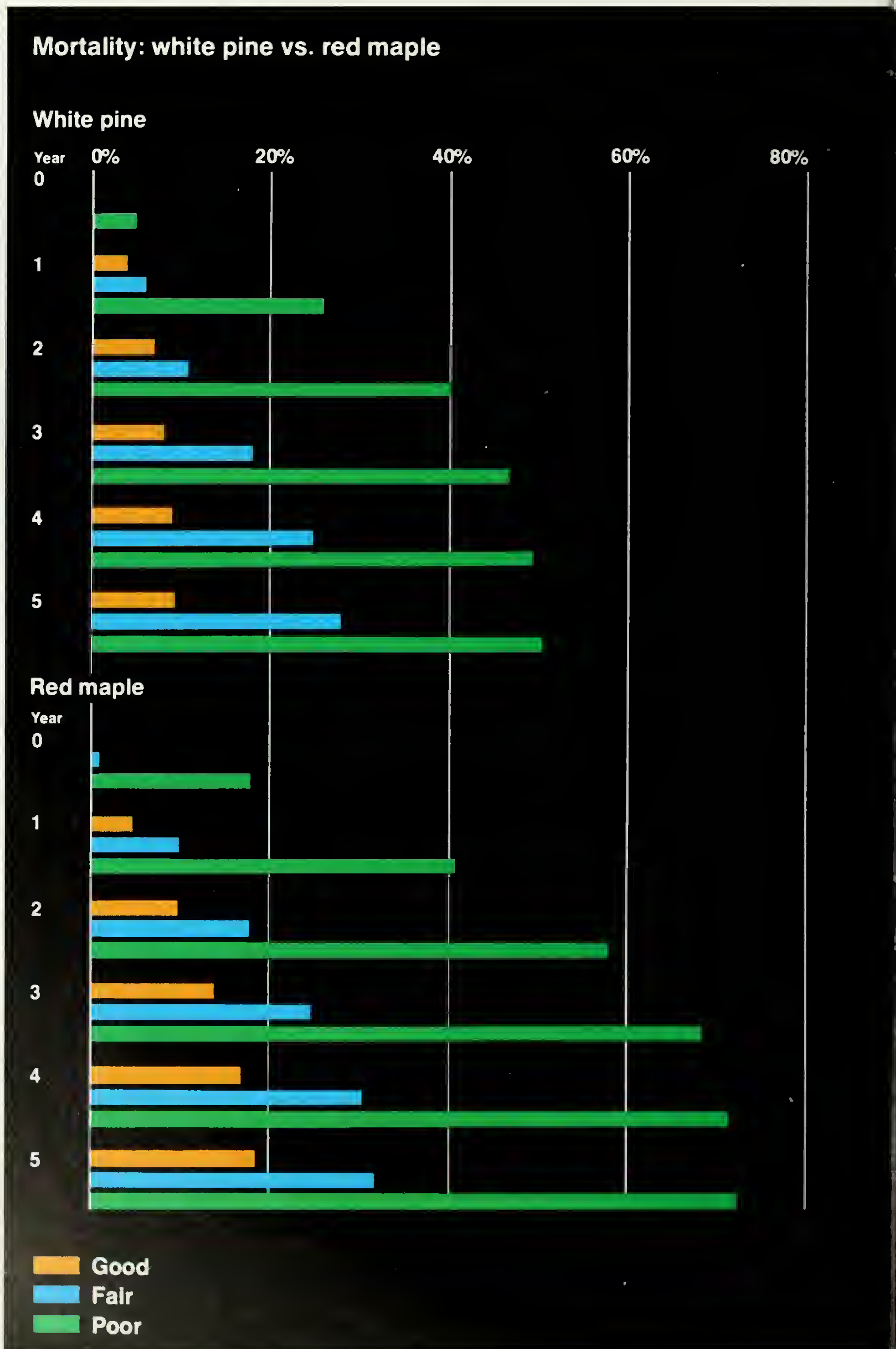


Figure 14.
Mortality among white pine and red maple trees during the 5 years after one heavy defoliation by the gypsy moth. Generally speaking, conifers are considered to be less tolerant of defoliation than hardwoods. In this case, though, mortality following defoliation was considerably lower among the pines than among the red maples.

About half of the living trees in the Melrose Highlands forest were favored-food trees in 1911, shortly after most of this forest was first invaded by the gypsy moth. By 1921, the proportion of these trees in the forest had been reduced to about one-third, largely through heavy and repeated defoliation (fig. 15). Differential mortality among favored and less favored trees clearly reduced the susceptibility of this forest to further outbreaks.

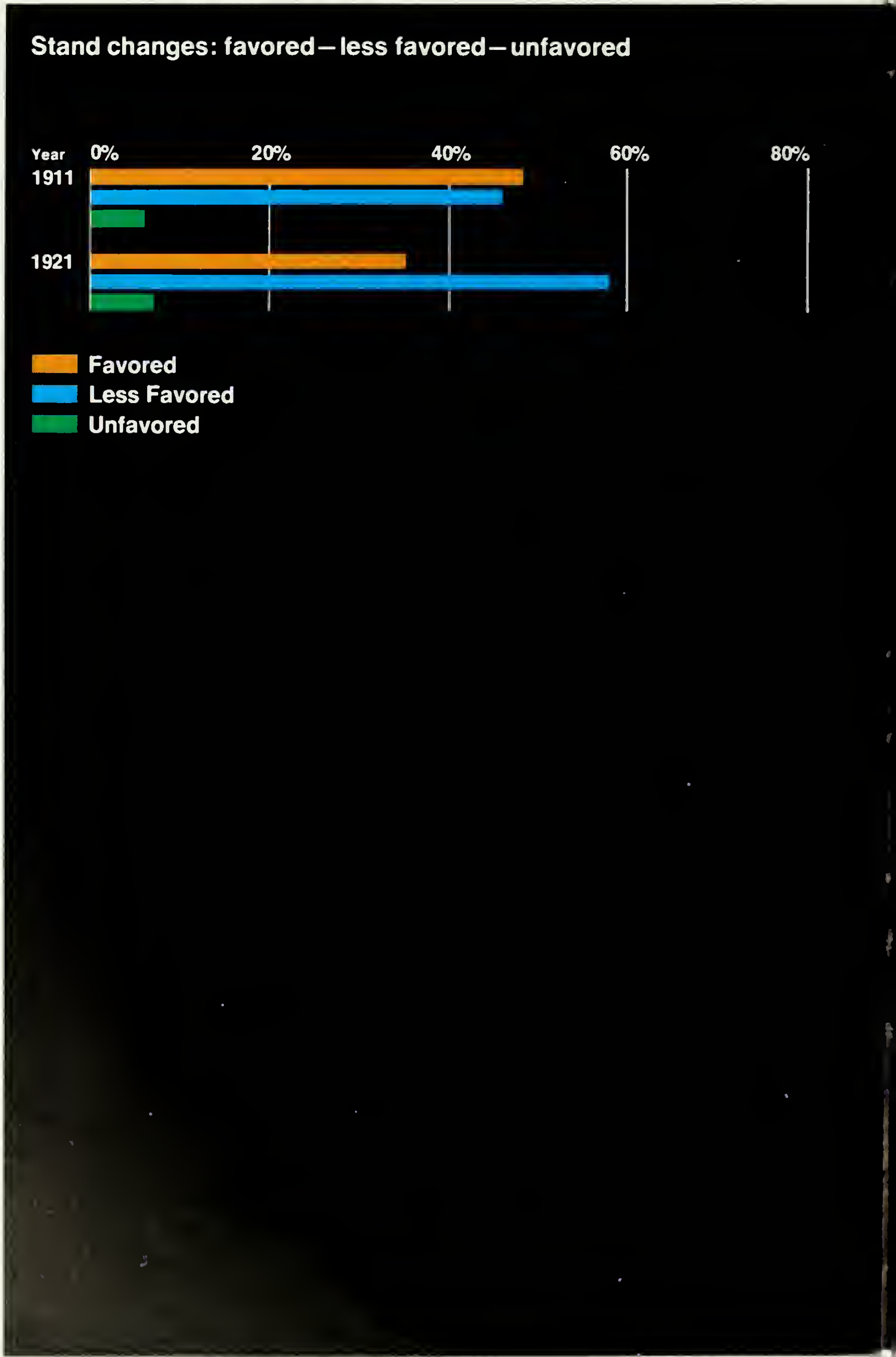


Figure 15.
Differential loss rates among favored and less favored trees tended to create residual stands in the composite forest that were less susceptible to defoliation than those present originally. Surprisingly, trees that are hardly ever defoliated by the gypsy moth did not become more prominant in this forest during the accelerated tree mortality of 1911-21, but this was due chiefly to extremely high mortality from old age among the pioneer redcedars.

Forest Succession and the Gypsy Moth

Earlier, I noted that unresolved questions about the nature of the gypsy moth problem were central to the long controversy over the proper management of this pest.

Unquestionably, heavy and repeated defoliation by the gypsy moth has sometimes produced catastrophic changes in the forest. But what sorts of future forest changes might be initiated by these current responses? People do not usually consider such questions, but forest managers clearly need a long-term perspective on the dynamic relationships between growing forest stands and pests such as this. Fortunately, at least in broad outline, the long-range biological consequences of forest invasion by the gypsy moth now seem predictable. They result from an interplay between defoliation and forest succession—the natural processes that lead inevitably to changes in the forest.

Climate, site, and vegetation

In general, the eastern hardwood forest, which covers some 235 million acres, has developed in response to climate, site conditions, and prior vegetational patterns.

Although both seasonal precipitation and the length of the growing season vary greatly across this enormous area, this great deciduous forest owes its overall character to the relatively *restricted* range in these two climatic variables. In a very general way, this forest is limited on the west by decreasing moisture and on the north by short growing seasons and extreme low temperatures in midwinter. To the south, the forest grades eventually into subtropical hardwoods.

Within a given climatic regime, the presence and distribution of specific plant communities are determined not only by local climate and soil conditions, but also by the effects of elevation, slope, aspect, and other site factors.

Unless some disturbing influence comes along, changes in an established plant community are controlled largely by its reactions to shading, competition for light, moisture, and nutrients, and modification of the soil. For example, all shrubs, seedlings, and other ground cover plants whose foliage is well below the level of the overall forest canopy must be able to complete their life processes in the shade produced by that canopy. As the forest grows and a continuous overstory canopy forms, only plants that can live and reproduce in shaded places will inhabit these understory layers. Consequently, systematic changes are bound to occur in the overall composition of a young forest. Such changes may seem imperceptibly slow, at first glance, but they can often be observed firsthand.

Consider, for example, the periphery of a field that has recently been abandoned for agriculture. In such places, you may be able to see for yourself where pioneer woody plants such as gray birch have been invading the area. You may also notice that many of these pioneers do not reproduce themselves under their own shade. In all probability, they will be replaced by species that can establish themselves under these woody pioneers. These new species are said to be more "shade tolerant."

If there is no disturbance, this process of one plant community succeeding another (plant succession) will continue until one community is able to perpetuate itself on the site indefinitely. This is called the climax community for the site. If this climax community is destroyed, it will usually develop once again, given enough time, if both the climate and the total living resource have remained essentially unchanged.

Forest influences

In the preceding section, I said that *if there is no disturbance* one plant community will continue to replace another until the climax community for that site is reached.

But forest disturbance is commonplace. People especially have changed and shaped this forest enormously. Most people probably think that the early European explorers of eastern North America journeyed through a forest unaltered in any substantial way by human activities. In fact, the Indians played a major role in determining the character of much of this forest. Early records show that the Indians frequently set light groundfires, primarily to aid their free movement and improve hunting.

Most of us scarcely associate States like Connecticut, Rhode Island, and New York with the agricultural heartland of North America, and with good reason. Many years ago, though, most of southern New England and New York was open farmland. But by 1850 portions of this landscape were beginning to be abandoned as competition from the fertile soils of newer farmlands to the west became more severe. In all, many millions of acres in this area were abandoned during the century between 1850 and 1950.

Besides what often proved to be a transient agriculture, two other human influences contributed to

Figure 16.
A typical eastern hardwood stand in central New England. Most such forests originated from abandoned farms, heavy cutting, and wildfire. They often contain many species in the forest canopy, but most stands are essentially even-aged and somewhere between 50 and 90 years old. These forests are highly complex biological communities.

the deforestation of much of the Northeast. These were extensive cutting and the severe, unintentional wildfires that often accompanied it or followed in its wake.

Together, transient agricultural activities, a heavy demand for wood, and wildfire removed an earlier forest from much of the land. Inevitably, forest succession has returned much of this land to forest once again. Within the past 100 years, for example, the proportion of forest land in both Rhode Island and Connecticut has doubled.

Currently, much of the northeastern United States is covered by a young first-generation forest (fig. 16). Certainly people will continue to play a role in shaping this living landscape, but I do not think that many of these young forests will be removed to make room for agriculture. Rather, many of them will be allowed to continue their growth and maturation.

Because their activities have played a dominant role in shaping the current forest, I have emphasized people as a forest influence. But the dynamic action of factors such as wind, naturally occurring wildfire, insects, and disease have all left their imprint on this forest. Undoubtedly, the chestnut blight has been chief among these influences during this century, at least within what was once called the oak-chestnut type.

Figure 17.
A forest under heavy attack by the gypsy moth. Although these trees are now being stripped of their foliage, they will produce a new crop of leaves in a few weeks. Understory vegetation and trees less favored by the insect will benefit from increases in light, moisture, and nutrient availability.

Chestnut blight has not eliminated the American chestnut from the eastern hardwood forest, but it *has* essentially removed these once majestic trees from the overstory. Sprouting continues, since the roots of the chestnut are not killed by the pathogen. In general, though, the place of this tree in the forest canopy has been taken over by other species.

Defoliation by insects such as the gypsy moth does not usually have such a dramatic impact on the forest as a disease like chestnut blight. Rather, both the less favored food species and the understory vegetation may benefit indirectly from the defoliation through increases in light, moisture, and nutrients (fig. 17). If continued, defoliation may result not only in the death or drastic decline of many of the overstory trees, but also in a definite and even dramatic stimulation of less favored species (fig. 18).

Figure 18.
This stand has been heavily defoliated for at least 2 years in succession. The gypsy moth population has now collapsed, but serious twig and branch dieback are evident. Secondary invaders, such as the two-lined chestnut borer and the shoestring fungus will continue to attack many of these trees. Even with abundant seasonal precipitation, many of these trees will die; a drought now would be disastrous to the damaged trees. Understory vegetation has definitely responded to this removal of much of the overstory foliage. Although chance can play a major role in the specific composition of this understory vegetation, it will probably contain a smaller percentage of favored-food species than the overstory.

Forest succession

Various oak species are now the dominant vegetation across much of the eastern hardwood forest. Many of these stands originated from sprouts after heavy cutting and wildfire. Temporarily, the proportion of oak in the overstory of such stands may increase somewhat because of naturally-occurring mortality among some of the relatively short-lived pioneer species, such as aspen and gray or paper birch. Except under exceptionally dry site conditions, however, successional changes within many of these first-generation oak stands will gradually lead toward a higher proportion of shade-tolerant species, such as sugar maple, American beech, and eastern hemlock, even without the gypsy moth. Within such stands, defoliation-induced changes in the forest have been surprisingly similar to those that might be expected from natural succession (fig. 19).

In contrast to the above, oak stands on the drier sites may represent climax, or at least relatively stable subclimax, communities. Two such dry-site oak types are the chestnut-oak forest, commonly found in the Northeastern States on dry rocky ridges, and the pine-oak forests of the excessively drained sands of the Atlantic coastal plain.

Figure 19.
A young mixed hardwood stand. Composite view of an eastern hardwood forest on a better growing site. This first-generation forest may be highly susceptible to defoliation. However, successional changes, which gradually reduce this defoliation-proneness even without the gypsy moth, are actually accelerated by defoliation.

Although the stands growing on chestnut-oak ridges may have little inherent value for timber, they frequently provide conditions that allow a low-density gypsy moth population to increase to damaging levels. For this reason, such stands can serve as central points for the spread of future outbreaks. Unfortunately, the chestnut-oak community growing on such sites is relatively stable, in terms of forest succession. Repeated defoliation of the forests growing on these ridges could conceivably lead not only to extensive tree mortality but also to the forest's reversion to an earlier succession stage—probably a heath-type plant community, wherein woody shrubs such as blueberry would tend to be the dominant vegetation. This management problem is almost certain to become more serious as the gypsy moth moves farther south along the Appalachian Mountains.

Oaks are climax species on the excessively drained sandy soils of the Atlantic coastal plain. In southern New Jersey, for example, cleared areas usually develop into shortleaf or pitch pine stands. In such cases, oaks come in after the pine is well established. By the time the pine stand is 50 to 55 years old, a definite hardwood understory has formed. Pine seedlings are few and hardwood seedlings are abundant. Again, if undisturbed these oaks and their descendants will continue to occupy such sites indefinitely (fig. 20).

Clearly, defoliation of *any* tree species is likely to be economically detrimental in a largely urbanized or recreation-oriented area. But oaks are often referred to as weeds in the commercial pine-oak forests that cover so much of the Atlantic coastal plain.

If further invasion of these pine-oak stands by the gypsy moth is inevitable—as I believe—the insect will probably cause heavy defoliation of the oak in many of these stands. Except in really rare instances, however,this defoliation will not cause even transient damage to the neighboring pines. Rather, defoliation of the hardwoods will generally tend to accelerate the growth of the pines. For the manager of a commercial pine-oak forest, the gypsy moth may prove to be an asset in the struggle with those "weed" oaks.

Figure 20.
A pine-oak forest of the Atlantic coastal plain. Composite view of another highly susceptible plant community, where plant succession leads toward an oak climax. Within commercial forests, at least, such stands are valued for their pine component; competing oaks are thought of as weeds. By holding back succession (favoring pines over oaks), the gypsy moth may prove to be a management asset in such stands.

After the Gypsy Moth

For most of us, encounters with the forest community beyond our doorstep are limited. Systematic change is occurring constantly in any living landscape, but we often think of the forest around us as a sort of mausoleum—static and unchanging.

Within the past century, a young forest has grown on land that man previously farmed, cut, burned, and abandoned. Forces are at work to further change this forest, and among the most remarkable of these forces are some of the forest-dwelling insects.

Outbreaks by the gypsy moth have tended to be most prolonged and damaging within the first few decades after the insect has invaded a new area. To date, defoliation and subsequent mortality have had more economic impact among roadside, park, and ornamental trees than among trees within the forest, although various forest losses have sometimes been directly attributable to heavy and repeated defoliation. Historically, at least, the defoliation caused by this insect has tended to become less damaging after a few decades (fig. 21).

We cannot hope to preserve the forest unchanged, any more than we can halt the ocean tides. Rather than treat each gypsy moth outbreak as a clear and unequivocal menace to the forest, we must ask ourselves whether the long-range influence of that outbreak would tend to be complementary or contrary to our own long-range management goals for that forest.

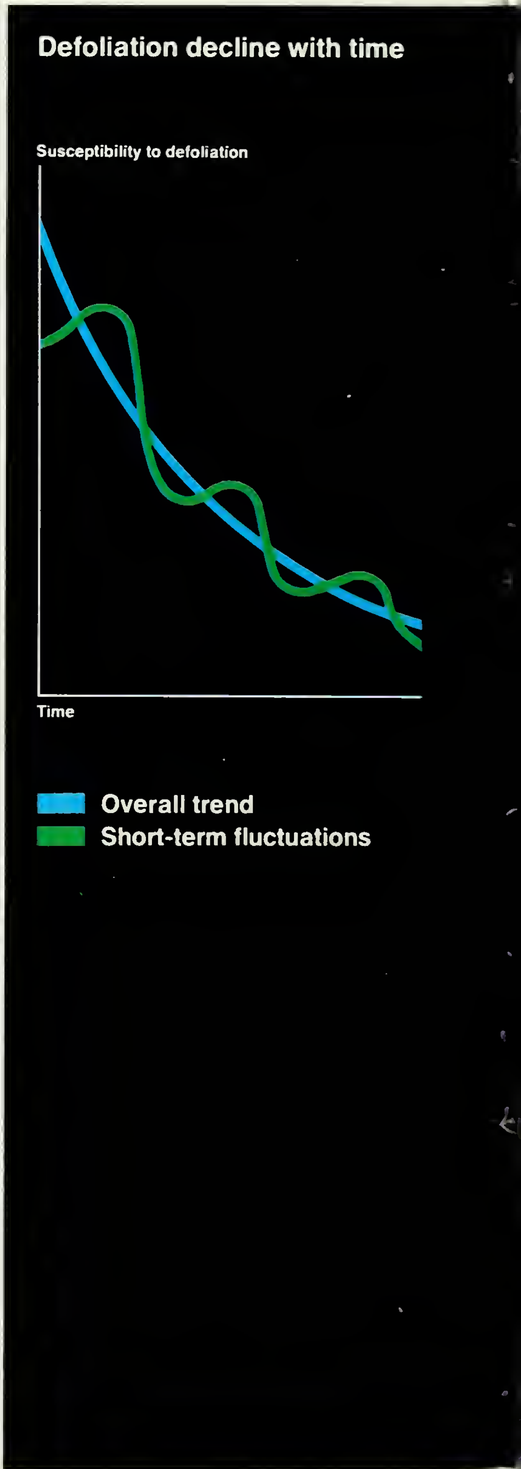


Figure 21.
The first outbreak by the gypsy moth after it invades a new area tends to have a more drastic effect on the stand than subsequent outbreaks. Except on unusually dry sites, changes in species composition after defoliation tend to reduce the stand's susceptibility to further defoliation and damage.

Suggestions for Further Reading

Bess, H. A., S. H. Spurr, and E. W. Littlefield.
1947. *Forest site conditions and the gypsy moth.* Harvard For. Bull. 22. 56 pp.

Braun, E. L.
1950. *Deciduous forests of eastern North America.* Hafner, New York. 596 pp.

Bromley, S. W.
1935. *The original forest types of southern New England.* Ecol. Monogr. 5: 61-89.

Campbell, R. W.
1974. *The gypsy moth and its natural enemies.* U.S. Dep. Agric., Agric. Info. Bull. 381. 27 pp.

Campbell, R. W.
1978. *Population dynamics: historical review.* In *The gypsy moth: research toward integrated pest management.* U.S. Dep. Agric. Tech. Bull. 1584. (In press).

Campbell, R. W. and R. J. Sloan.
1977. *Forest stand responses to defoliation by the gypsy moth.* For. Sci. Monogr. 19, 34 pp.

Daubenmire, R.
1968. *Plant communities.* Harper and Row, New York. 300 pp.

Keever, C.
1953. *Present composition of some stands in the former oak-chestnut forest in the southern Blue Ridge Mountains.* Ecology 34: 44-54.

Little, S.
1974. *Effects of fire on temperate forests: northeastern United States.* In *Fire and Ecosystems.* pp. 225-250. Academic Press. New York.

Marquis, D. A.
1977. *Silviculture of eastern hardwoods.* In *The scientific base for silviculture and management decisions in the National Forest System.* U.S. Dep. Agric. For. Serv., Washington, D.C. pp. 29-38.

Mattson, W. J. and N. D. Addy.
1975. *Phytophagous insects as regulators of forest primary production.* Science 190: 515-522.

Niering, W. A.
1953. *The past and present vegetation of Highpoint State Park, New Jersey.* Ecol. Monogr. 23: 127-148.

Spurr, S. H.
1956. *Forest associations of the Harvard Forest.* Ecol. Monogr. 26: 245-262.

☆ U.S. GOVERNMENT PRINTING OFFICE : 1979 O—286-823

Acknowledgments

I salute the pioneering efforts of the workers at the Melrose Highlands Laboratory. Between 1911 and 1931, they accumulated a formidable body of gypsy moth/forest records. Much later, between 1973 and 1975, my friend and colleague Ron Sloan worked tirelessly to bring order and structure to these long-forgotten records. Finally, I thank illustrator Robert W. Brown and photographer Richard C. Rollinson. Their work provides vivid visual images of the gypsy moth as an influence on the ever-changing forest.